FEEDING HABITS OF THE BIGEYE THRESHER SHARK (*ALOPIAS SUPERCILIOSUS*) SAMPLED FROM THE CALIFORNIA-BASED DRIFT GILLNET FISHERY

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ABSTRACT

The diet of the bigeye thresher shark (*Alopias superciliosus*) was investigated by quantifying the stomach contents of sharks taken in the California-based drift gillnet fishery. Fishery observers collected stomachs of sharks ranging in size from 147 to 230 cm fork length during the 1998–99 and 2002–06 seasons in pelagic waters between the U.S.-Mexico border and Cape Mendocino, California. The frequency of prey items in stomachs by weight, number, and occurrence was determined and used to calculate two indices of dietary preference: the geometric index of importance (GII) and index of relative importance (IRI). Of 26 stomachs examined, 23 contained food items representing 20 taxa, indicating a broad trophic spectrum. Overall, the two indices consistently ranked the relative importance of prey items. Of the 10 taxa of teleosts found in the diet, fish of the family barracudinas (Paralepididae) represented the most important prey item (GII = 52.8; %IRI = 45.98), followed by Pacific hake (*Merluccius productus*; GII = 38.4; %IRI = 24.23), Pacific saury (*Cololabis saira*; GII = 22.2; %IRI = 8.08), Pacific mackerel (*Scomber japonicus*; GII = 17.3; %IRI = 3.92), and northern anchovy (*Engraulis mordax*; GII = 16.0; %IRI = 3.93). Of the eight taxa of cephalopods, jumbo squid (*Dosidicus gigas*; GII = 15.5; %IRI =3.61) and *Gonatus* spp. squid (GII = 11.0; %IRI = 0.63) were proportionately highest in ranking. The remaining two taxa were both crustaceans. Despite a sample size inadequate for characterizing the full breadth of the bigeye thresher diet, these data demonstrate that bigeye thresher sharks have a diverse diet and may feed opportunistically on locally and temporally available prey, including epipelagic, mesopelagic, epi–benthic, and deep–scattering–layer species. These data are consistent with fishery and electronic tracking data which demonstrate that the bigeye thresher shark is predominately a deep-water species, but spends time both within the deep-scattering and the mixed–surface layers.

INTRODUCTION

The bigeye thresher shark (*Alopias superciliosus*) occurs in tropical and temperate seas world-wide (Compagno 2001). An epipelagic and mesopelagic species, it is found primarily in oceanic and neritic waters, over continental and insular shelves where surface temperatures range from 15°–26°C (Gruber and Compagno 1981; Compagno 2001). Within the U.S. West Coast Exclusive Economic Zone (EEZ) it is commonly taken in the drift gillnet fishery that targets swordfish and has been caught from the U.S.-Mexico border to 45°N latitude. Bigeye thresher shark co-occurs in the drift gillnet catch with the common thresher shark (*Alopias vulpinus*) but is generally taken in offshore waters, whereas the common thresher is predominately found in near-shore waters. Annual U.S. West Coast landings of bigeye thresher sharks have averaged 26 mt since 1981 (range: 0 to 96 mt), with most animals taken between August and November (Hanan et al. 1993). In the Hawaii-based longline fisheries for swordfish and tunas, the bigeye thresher is the second most common shark encountered with relatively greater numbers caught in the deeper tuna sets (C. Boggs and W. Walsh, NOAA Pacific Islands Regional Observer Program, pers. comm.). Although they appear to have a broad geographic range, little is known of their migratory behavior and stock structure.

The vertical behavior of bigeye thresher sharks in the Pacific Ocean has been studied using electronic tags (Nakano et al. 2003; Musyl et al. 2004; Weng and Block 2004). Although only a few animals were tagged in these studies, they demonstrated distinct crepuscular vertical migrations, descending near sunrise and ascending near sunset. During the day, sharks were typically at depths between 200–550 m in 6°–12°C water and then shifted to shallower depths (10–130 m) and warmer waters (15°–26°C) at night. Their vertical behavior was similar to that of the megamouth shark, *Megachasma pelagios* (Nelson et al. 1997) and swordfish, *Xiphias gladius* (Carey and Robison 1981), both of which are believed to forage within the deep scattering layer (DSL).

Feeding behavior of bigeye thresher sharks is likely linked to a suite of unique morphological characteristics. Like the other thresher sharks, the bigeye thresher has a long caudal fin with which it seems to stun its prey; individuals are often tail-hooked when taken on longlines (Springer 1961; Compagno 2001). Unlike the other threshers, the large eyes of the bigeye thresher extend

onto the dorsal surface of the head, suggesting binocular vision both forward and overhead, which would enable foraging from below (Compagno 2001). Finally, the presence of a cranial rete mirabile indicates a mechanism for heat conservation and cranial endothermy (Carey and Teal 1969; Carey et al. 1971; Carey 1982; Block and Carey 1985; Weng and Block 2004). Elevated eye temperatures have been found to enhance foraging in cold waters by improving visual acuity (Fritsches et al. 2005).

Despite interest in their foraging ecology and their relatively common occurrence in a number of fisheries, little is known about the feeding habits of the bigeye thresher. Several studies report on stomach contents of bigeye threshers, but many of these describe only one or a few specimens (Fitch and Craig 1964; Bass et al. 1975; Stillwell and Casey 1976; Gruber and Compagno 1981; Polo-Silva et al. 2007). In addition, only one individual from all of these studies was from the northeast Pacific Ocean (Fitch and Craig 1964), where bigeye threshers are taken in longline fisheries on the high seas and in drift- and set-net fisheries closer to shore. This study reports on the foraging ecology of bigeye threshers caught in the pelagic drift gillnet swordfish fishery off the California coast based on their stomach contents.

METHODS

Stomachs of bigeye thresher sharks were collected during the 1998–99 and 2002–06 fishing seasons by NOAA Fisheries observers aboard commercial drift gillnet vessels. The drift gillnet fishery operates from 15 August to 31 January in U.S. federal waters from the U.S.-Mexico border to the Washington-Oregon state border. The majority of the fishery currently operates in the Southern California Bight (SCB). All vessels are required to fish with large mesh drift gillnets (≥14 in. stretched mesh) that are set overnight and retrieved in the morning. The nets are typically between 50 to 75 m deep and are set 12 m below the surface. The date, time, location, water temperature, characteristics of the net, fork length, and sex were recorded for each specimen. Stomachs were removed, frozen onboard, and later transferred to the Southwest Fisheries Science Center where they were processed within 6 months.

Stomach contents were sorted, digestive states noted, and prey were analyzed to the lowest possible taxon following the methods of Preti et al. (2001) and using keys when necessary to identify species from hard parts (Clothier 1950; Iverson and Pinkas 1970). Data were pooled across all years and analyzed by prey taxa for relative measures of prey quantities (RMPQs) as follows: percent occurrence by number (%N), percent frequency-of-occurrence (%F), and percent occurrence by weight (%W) of prey items. Weight was the actual weight of the prey remains, not the estimated weight of prey at inges-

tion. The value %N is the number of individuals of a specific taxon found in all stomachs divided by the total number of all prey found multiplied by 100; %F is the number of stomachs containing prey of a specific taxon divided by the total number of stomachs containing prey multiplied by 100; %W is the total weight of all remains of a specific taxon divided by the total weight of all prey remains found multiplied by 100 (Hyslop 1980; Preti et al. 2001). Empty stomachs, slurry, and detritus were not used when calculating percentages. The values listed above were used to calculate the three-dimensional dietary indices: the geometric index of importance (GII) and the index of relative importance (IRI).

The GII (Assis 1996; Mohan and Sankaran 1988; Fernández and Oyarzun 2001) and the IRI (Pinkas et al. 1971) were used to rank prey and to graphically represent the relative measures of prey quantity. We used each method to examine only the relative difference in ranking of prey types, because individual index values are not directly comparable.

The GII, in its generalized form, is calculated as:

$$\text{GII}_j = \frac{\left(\sum_{i=1}^{n} V_i \right)_j}{\sqrt{n}},\tag{1}$$

where GII_j = index value for the j-th prey category, V_i = the magnitude of the vector for the i-th RMPQ of the j-th prey category, and n = the number of RMPQs used in the analysis. In our study this is expressed as:

$$\text{GII}_j = (\%\text{N}_j + \%\text{W}_j + \%\text{F}_j) / \sqrt{3}\tag{2}$$

The IRI for the j-th prey category is calculated as:

$$\text{IRI}_j = (\%\text{N}_j + \%\text{W}_j) * \%\text{F}_j .\tag{3}$$

The IRI value was converted to a percentage in order to facilitate comparisons among studies (Cortés 1997). Because the GII is a general form which can be used with any number of different types of RMPQs (Assis 1996), comparisons among studies is not always possible. Furthermore, %GII, which is the geometric mean of the RMPQs used and differs from GII by a single factor, does not necessarily sum to 100 when each individual RMPQ does not sum to 100. Therefore, we chose not to convert GII values to percentages as they would have had no added value, but they can easily be calculated from the data provided.

Randomized cumulative prey curves were constructed to examine trophic diversity and determine if sample size was sufficient to describe the full diet (Hurtubia 1973; Ferry and Cailliet 1996; Ferry et al. 1997; Gelsleichter et al. 1999; Yamaguchi and Taniuchi 2000). For this analysis, the order in which stomach contents were analyzed
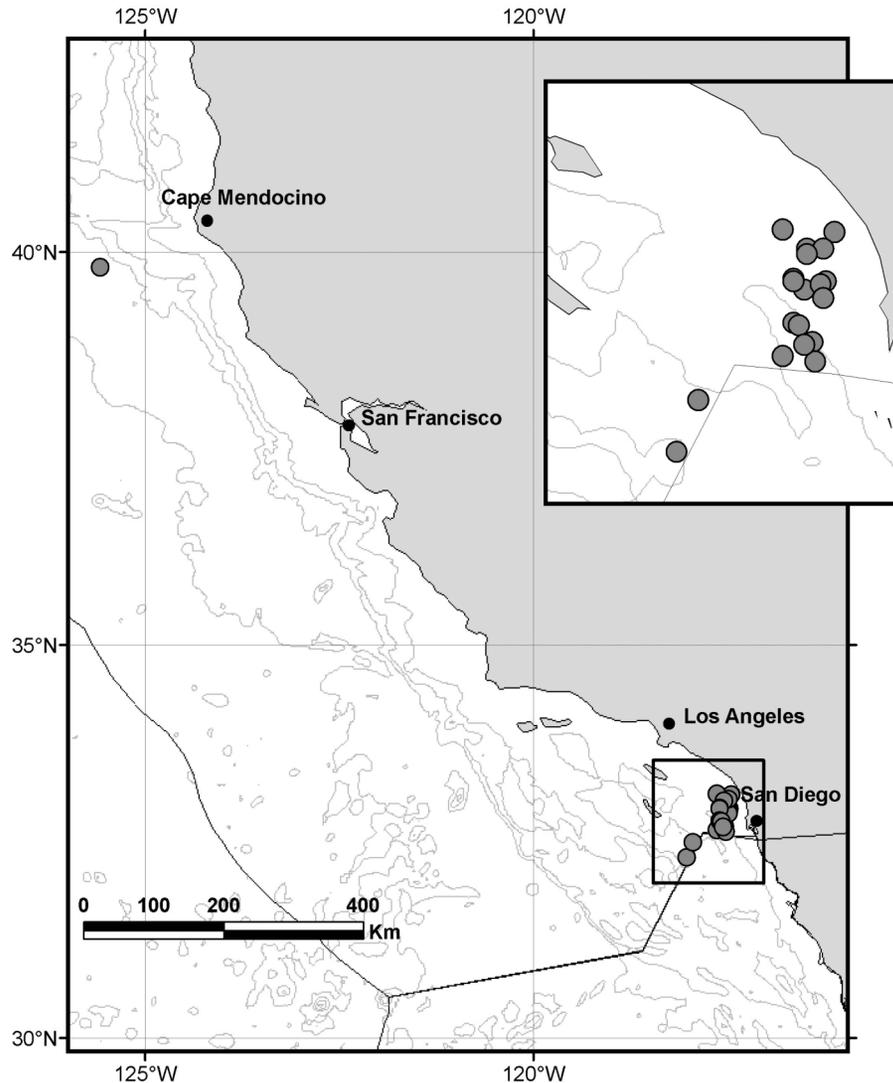
Figure 1.   Collection locations for bigeye thresher shark (*Alopias superciliosus*) stomach samples, 1998–2006.

was randomized 10 times and the mean and standard error of the number of new prey observed was plotted for each consecutive stomach. A curve approaching an asymptote with low variability indicates that the number of stomachs examined was sufficient to characterize the diet.

RESULTS

Over the course of the study, 26 stomachs were collected during 18 observed trips. Most stomachs (18) were collected during the 2005 fishing season; two were collected during each of the 1999 and 2006 seasons, and one stomach from each of the 1998, 2002, 2003, and 2004 seasons. One shark was sampled in 1998 offshore of Cape Mendocino, California, and the rest were sampled in the SCB within 185 km of San Diego (fig. 1). Bottom depths ranged from 475 to 3327 m. Water tem-

perature ranged from 16.0° to 21.1°C. Fishing depth of the nets in which the sharks were caught ranged from 11 m down to roughly 100 m, although the observers did not note where in the net the sharks were caught. The sharks ranged in size from 147 cm to 230 cm fork length (FL). Eight sharks were female, 17 male, and one was of unknown sex (fig. 2). Based on maturity studies of bigeye threshers in the western Pacific Ocean (Chen et al. 1997; Liu et al. 1998), nine of the males sampled were reproductively mature and all others sampled were subadults.

Of the 26 stomachs examined, 23 contained food representing a total of 20 taxa (tab. 1). Seventy-eight percent of the food items were in an advanced state of digestion; they were identified either by body parts that could not be reconstructed into measurable prey, hard parts only, or nearly digested remains. Consequently, in
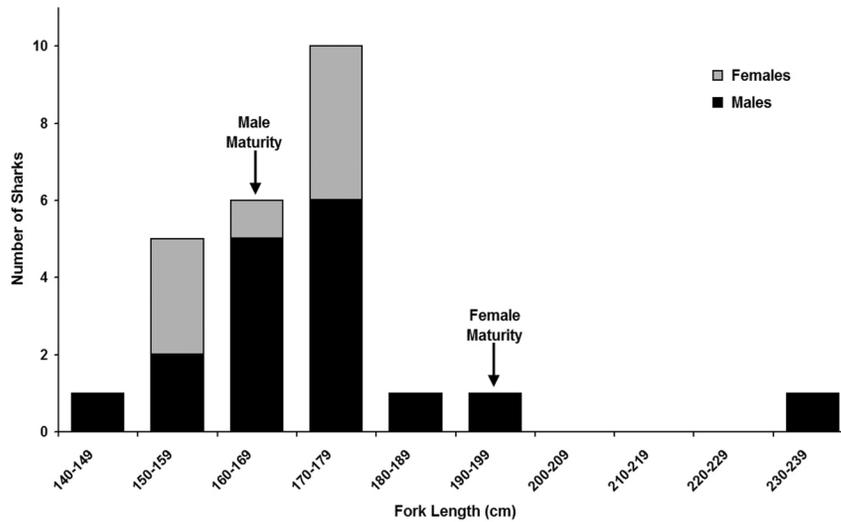
Figure 2.   Length-frequency distribution of bigeye thresher sharks (*Alopias superciliosus*) sampled in the diet study. *N*=25 sharks; fork length and sex were not determined for one of the 26 sharks in the study.

TABLE 1

Quantitative prey composition of the bigeye thresher shark (*Alopias superciliosus*) along the California Coast. A total of 23 stomachs containing food and three without food were examined. Prey items are shown by decreasing values of GII. See methods for descriptions of the measured values.

Prey species	W (g)	%W	N	%N	F	%F	GII	IRI	%IRI
Barracudinas, Paralepididae	2076.9	21.62	69	26.34	10	43.48	52.79	2084.96	45.98
Pacific hake, *Merluccius productus*	1378.4	14.35	57	21.76	7	30.43	38.42	1098.80	24.23
Pacific saury, *Cololabis saira*	631.6	6.57	38	14.50	4	17.39	22.21	366.57	8.08
Pacific mackerel, *Scomber japonicus*	383.3	3.99	11	4.20	5	21.74	17.28	178.00	3.93
Northern anchovy, *Engraulis mordax*	141.8	1.48	23	8.78	4	17.39	15.96	178.34	3.93
Unidentified Teleostei	125.0	1.30	22	8.40	4	17.39	15.64	168.66	3.72
Jumbo squid, *Dosidicus gigas*	282.1	2.94	17	6.49	4	17.39	15.48	163.91	3.62
Jack mackerel, *Trachurus symmetricus*	1576.0	16.40	3	1.15	1	4.35	12.64	76.30	1.68
King-of-the-salmon, *Trachipterus altivelis*	1503.7	15.65	3	1.15	1	4.35	12.21	73.03	1.61
Bocaccio rockfish, *Sebastes paucispinis*	1404.4	14.62	1	0.38	1	4.35	11.17	65.22	1.44
Gonatus spp.	10.5	0.11	4	1.53	4	17.39	10.99	28.46	0.63
Flowervase jewell squid, *Histioteuthis dofleini*	23.3	0.24	3	1.15	3	13.04	8.33	18.10	0.40
Unidentified Teuthoidea	40.8	0.42	2	0.76	2	8.70	5.71	10.33	0.23
Market squid, *Loligo opalescens*	21.8	0.23	2	0.76	2	8.70	5.59	8.61	0.19
Pacific sardine, *Sardinops sagax*	5.5	0.06	2	0.76	2	8.70	5.49	7.14	0.16
Unidentified Crustacea	2.0	0.02	1	0.38	1	4.35	2.74	1.75	0.04
Boreopacific gonate squid, *Gonatopsis borealis*	0.01	0.00	1	0.38	1	4.35	2.73	1.66	0.04
Octopoteuthis sp.	0.01	0.00	1	0.38	1	4.35	2.73	1.66	0.04
Cranchia, *Cranchia scabra*	0.01	0.00	1	0.38	1	4.35	2.73	1.66	0.04
Pelagic red crab, *Pleuroncodes planipes*	0.01	0.00	1	0.38	1	4.35	2.73	1.66	0.04

some cases, for example for *Gonatus* spp. squid, the ranking of the relative indices of importance may be lower than for other prey found intact, but in fewer stomachs. Table 1 lists each of the RMPQs for all prey found, as well as the calculated three-dimensional relative indices of importance. RMPQs for the most important prey taxa, as determined by the highest GII and %IRI rankings or the frequency of occurrence in four or more stomachs, is also shown graphically (fig. 3).

Rankings based on GII and IRI were nearly identical (tab. 1). Teleosts of the family barracudinas (Paralepididae) were the most important prey item in number, frequency, weight, and based on the combined indices. Almost half of the barracudinas remains (44%) were identified as duckbill barracudina (*Magnisudis atlantica*) using otoliths. Other dominant teleost prey included Pacific hake (*Merluccius productus*), Pacific saury (*Cololabis saira*), Pacific mackerel (*Scomber japonicus*), and northern anchovy (*Engraulis mordax*). King-of-the-salmon (*Trachipterus altivelis*) was only found in the shark caught farthest north, off Cape Mendocino, California. Eight taxa of cephalopods were also found with jumbo squid (*Dosidicus gigas*) and Gonatus spp. squid making the greatest contributions to the diet. One unidentified crustacean and remains of
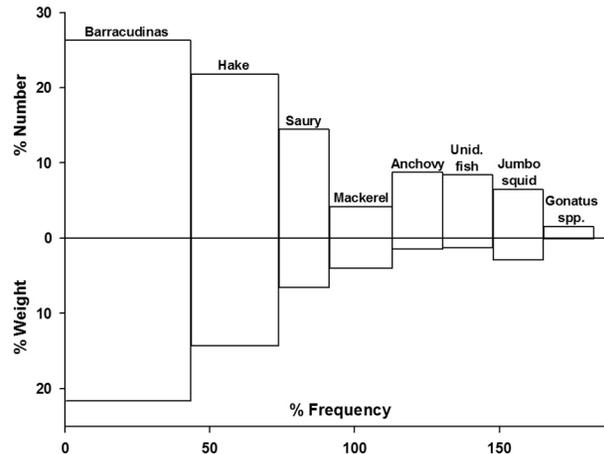
Figure 3.   Graphical representation of bigeye thresher shark (*Alopias superciliosus*) diet using RMPQ values % weight, % frequency of occurrence, and % number for the major prey items.
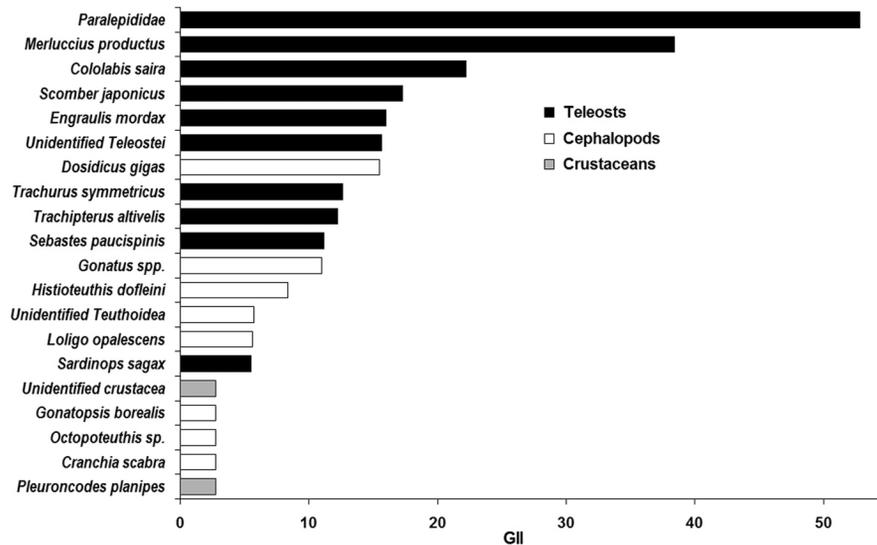

Figure 4.   Results of geometric index of importance (GII) analyses for the 20 prey taxa (*N* = 23 stomachs containing prey).

a pelagic red crab (*Pleuroncodes planipes*) were also found (tab. 1; fig. 4).

Cumulative prey curves described a generally increasing relationship that did not reach full asymptotic stabilization (fig. 5). Thus, our sample size may not have been sufficient to describe the overall trophic diversity of this species' diet. Given the low sample size, further subdivision of the samples by year, sex, or size class would not have been appropriate to examine interannual, sex-specific, or ontogenetic differences in diets for this species.

DISCUSSION

General Findings and Study Limitations

This is the first study to report on the diet of the bigeye thresher shark in the U.S. West Coast EEZ with the exception of an early report including only one animal (Fitch and Craig 1964). Results suggest that bigeye thresher sharks are opportunistic feeders, foraging on diverse species covering a broad range of habitats. Overall, 20 species of prey occurred in only 23 stomachs. The prey identified included fish, cephalopods, and crustaceans from a range of habitats. The species making up the greatest component of the bigeye thresher shark diet in southern California were mesopelagic and epipelagic teleosts and are listed in order of importance: barracudinas, Pacific hake, Pacific saury, Pacific mackerel, and northern anchovy. At least eight cephalopod species were also observed, although most species were found in only a few stomachs. Of the cephalopods, the jumbo squid, which has shown up in large numbers off the California coast in recent years (Field et al. 2007), was the highest ranked
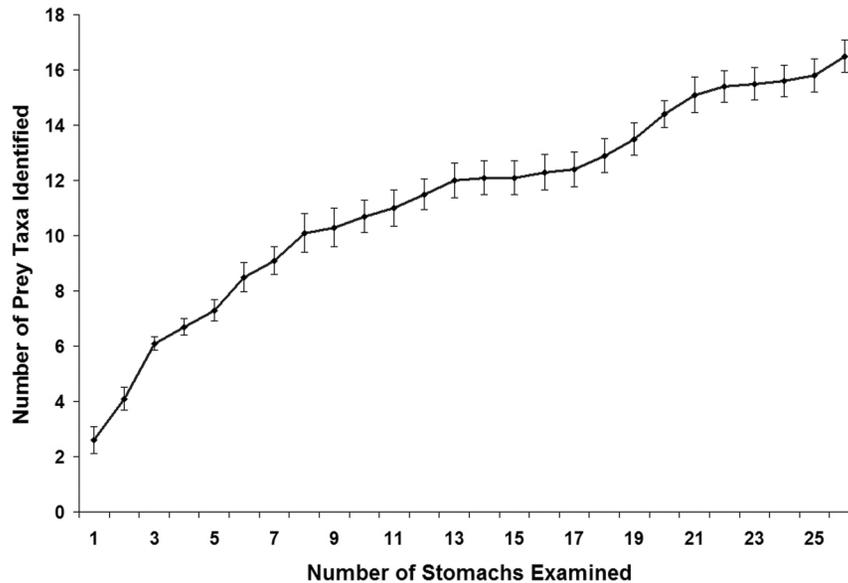
Figure 5.   Randomized cumulative prey curve for the bigeye thresher shark (*Alopias superciliosus*) diet sample. Mean values are plotted; error bars represent ± SE (*N* = 26 stomachs examined). The curve has not reached an asymptote and the error bars are not declining indicating that the sample size may be insufficient to fully describe the diet.

species. Squid from the genus *Gonatus* were also important. Crustaceans appear not to be highly important in the SCB over the sampling season; only two taxa were found, each in only one stomach.

Although this study provides some of the first insights into the foraging ecology and biology of bigeye thresher sharks off the California coast, we caution that the sample size may have been insufficient to fully characterize the bigeye thresher diet in this area. Even more novel prey would have likely been encountered as sample size increased, as indicated by the mean cumulative prey curve. Also, because most of the samples were collected in a single season, interannual comparisons were not possible, nor were examinations of ontogenetic or sex-specific differences in foraging ecology. Continued sampling is ongoing in order to address these limitations.

Sampling sufficient numbers of bigeye thresher sharks off the California coast is difficult given that the encounter rates are relatively low in this fishery and only 20% of the trips are observed. Sampling effort for this study has been variable. Prior to the 2005 season, observers only casually collected bigeye thresher stomachs. In 2004, bigeye threshers became a federally managed species under the Pacific Fishery Management Council's Fishery Management Plan for Highly Migratory Species, and consequently NOAA Fisheries asked observers to prioritize collecting bigeye thresher stomachs in order to learn more about their biology and ecology. Even with increased priority placed on collecting bigeye thresher samples, few specimens were collected in 2006, suggesting that differences in availability may have affected our sample sizes. We examined the nominal catch-per-unit-

effort (nCPUE) of bigeye threshers in the observed catch of the drift gillnet fishery over the study period (unpublished data; NOAA Southwest Region Fishery Observer Program). Nominal CPUE was highest at 0.33 sharks per set during the 2005 season. Oceanographic conditions could be one factor responsible for variations in bigeye thresher catch rates. We looked at both the El Niño Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) indices (http://cses.washington.edu/cig/pnwc/compensopdo.shtml; http://www.cdc.noaa.gov/people/klaus.wolter/MEI/) to determine whether El Niño, La Niña, or decadal regimes affected catch rates during the study period. There were mild El Niño conditions during fishing seasons 2002, 2004, and 2006, and La Niña conditions during 1998, 1999, and 2005. More significantly, there was a regime shift during the sampling period; 1999–2002 was a cool regime and 2003–05 was a warm regime based on the PDO index. Nominal CPUE was nearly an order of magnitude higher during the PDO warm phase (2003–06: nCPUE = 0.17 ± 0.10 sharks per set) than during the cool phase (1999–2002: nCPUE = 0.02 ± 0.003 sharks per set). But the ENSO index itself does not seem correlated with nCPUE, at least over the last decade. The three seasons with the highest nCPUE (2005, 2006, and 2003) are classified respectively as La Niña, El Niño, and neutral based on the ENSO index. Alternatively, the four seasons with the lowest nCPUE (2002, 1999, 2000, and 2001) are classified respectively as El Niño, two La Niñas, and neutral.

While the three-dimensional diet indices consistently ranked the top species, the use of these standard indices may misrepresent the importance of some prey. Each

RMPQ measures a different aspect of the diet (bulk versus number versus occurrence, in the case of the present study) and it has long been emphasized that each has its limitations and biases toward different aspects of the diet (Hyslop 1980; Cortés 1997). Furthermore, even the three-dimensional indices may alter conclusions about the importance of prey taxa when taxa are combined into generalized groups (Hansson 1998). We provide tables and analyses with the highest prey resolution possible allowing readers to calculate alternate indices of their choice.

We were not able to overcome the fact that indices may underrepresent prey identified by beaks or otoliths alone as a consequence of various stages of digestion in the stomachs. Unfortunately, the quantitative relationships between hard-part size and mass that would be necessary to calculate weight at ingestion are not available for all of the prey species.

A final aspect which limits conclusions about bigeye thresher foraging ecology is the lack of information on when and where feeding occurs. There are currently no data available about what time of day bigeye thresher sharks actually consume prey. Although the fishery in which the sharks were caught for the current study operates at night and fishes from roughly 12 m to 90 m deep, prey in advanced states of digestion as well as some fresh prey were found in the stomachs examined. Without information on how rapid digestion occurs and at what time and depth the fish were actually caught, it is not possible to further discern a precise measure of the time and depth of foraging.

Despite these limitations, these data comprise the most comprehensive study to date of the foraging ecology of bigeye threshers off the California coast.

Intraspecies Comparisons Among Areas

The results of this study demonstrate considerable overlap with other studies of bigeye thresher shark diets. Although many of the prey species differ, the most important items at most locations appear to be epipelagic and mesopelagic fish and squid. The only prior report on bigeye thresher diets in the North Pacific Ocean reported six Pacific hake (*Merluccius productus*) in the stomach of one specimen taken off California (Fitch and Craig 1964). In the present study, Pacific hake was the second most important prey. There are a number of interesting differences in the species composition observed both across and within ocean basins; while a small istiophorid was reported in one of 18 stomachs in the Atlantic Ocean (Stillwell and Casey 1976), none have yet been observed in the northeast Pacific Ocean (Fitch and Craig 1964; current study). It should be noted, however, that small istiophorids are not common in the area from which these samples were collected. The Atlantic study also reported that scombrids accounted for the greatest amount

of fish remains (27%), whereas in this study Pacific mackerel was present in only five stomachs and was less important than barracudinas, hake, and saury. Also, no elasmobranchs were found in the current study, although they occurred in the diet of a bigeye thresher off South Africa (Bass et al. 1975). Comparing the results from the SCB to Ecuador (Polo-Silva et al. 2007), where the only comprehensive study of bigeye thresher diets, in which each prey species was enumerated, has been conducted, mesopelagic and epipelagic fish and cephalopods were important in both areas. The most important prey species in the Ecuador study were silver drum (*Larimus argenteus*), south Pacific hake (*Merluccius gayi*), jumbo squid (*Dosidicus gigas*), and lamp fish (*Benthosema panamense*). A larger number of epi-benthic and reef-associated species were also found, presumably due to the habitat fished; the fishery sampled was a coastal artisanal fishery unlike the pelagic fishery sampled here. As in the present study, the number of prey species found was relatively high; the 107 bigeye thresher stomachs containing prey had a minimum of 27 different species in their stomachs.

Comparisons with Sympatric Species

The bigeye thresher shark co-occurs with the common thresher, shortfin mako (*Isurus oxyrinchus*), and blue shark (*Prionace glauca*) in the catch of the California drift gillnet fishery. A comparison of the bigeye thresher shark diet to that of other overlapping pelagic sharks demonstrates variability in both the number and types of species encountered in the diets.

Those species for which published diet information is available from California waters include the common thresher shark (Preti et al. 2001; Preti et al. 2004) and blue shark (Tricas 1979; Harvey 1989). Combined, the common thresher shark studies reported 21 prey taxa in 174 stomachs containing food; however, the diet was more diverse (20 taxa) during a warm-water year following El Niño (Preti et al. 2001) than during a more typical year (eight taxa; Preti et al. 2004). In both cases, the most important prey were epipelagic species such as northern anchovy, Pacific hake, Pacific sardine, Pacific mackerel, and market squid (*Loligo opalescens*). The two blue shark studies combined reported 37 prey taxa (identified at least to genera) in a total of 226 stomachs; prey included primarily fish, cephalopods, and crustaceans (Tricas 1979; Harvey 1989). While there were considerable differences in the species composition (13 taxa overlapped), the prey covered the same range of habitats including a number of epi-benthic species (spiny dogfish and rockfish), teleosts from the epipelagic zone (anchovy, herring, and jack mackerel), and fish and squid associated with the DSL (myctophids, *Dosidicus* and *Histioteuthis*). Based both on electronic tagging studies and the diet composition, the blue shark likely forages

on DSL-associated species both at night near the surface as well as during the day at depth (Harvey 1989; Carey and Scharold 1990).

Comparison of bigeye thresher, common thresher, and shortfin mako sharks' diets for a single season (2005–06) revealed the most prey taxa in the bigeye thresher sample, despite a smaller sample size (bigeye thresher: 14 prey taxa in 15 stomachs; mako shark: 11 prey taxa in 32 stomachs; common thresher: five prey taxa in 41 stomachs; Southwest Fisheries Science Center unpubl. results). The bigeye thresher appears to forage across habitats whereas more niche separation is apparent for the other species. The stomach contents of the common thresher were dominated by epipelagic species. Shortfin mako stomachs contained a large variety of taxa, including epipelagic and mesopelagic teleosts and cephalopods, but no epi-benthic species.

Swordfish, another obvious overlapping large pelagic species, is the target of the drift gillnet fishery. Based on electronic tagging studies in a few areas, the bigeye thresher demonstrates the same general diel vertical migration as swordfish (Carey and Robison 1981; Carey 1990; Nakano et al. 2003; Musyl et al. 2004; Weng and Block 2004). Swordfish also forage on many of the same prey (Mearns et al. 1981; Moteki et al. 2001; Markaida and Hochberg 2005); swordfish taken by drift gillnets in the SCB were found to feed predominately on northern anchovy (%IRI = 42.6) and Pacific hake (%IRI = 41.9; Mearns et al. 1981), both of which were identified in the top five prey for bigeye threshers in this study.

Ecology of the Main Prey Taxa

To further explore the foraging ecology of the bigeye thresher sharks, we considered the habitats and behaviors of the top prey species. Given the limitations associated with the RMPQs and indices, we examined the characteristics of the seven taxa that fell into the top 11 prey species for both the GII and %IRI and that were found in a minimum of four stomachs. These prey taxa include barracudinas, Pacific hake, Pacific saury, Pacific mackerel, northern anchovy, jumbo squid, and *Gonatus* spp. squid.

Based on the biology of the seven top taxa, it seems that bigeye thresher sharks forage across a range of habitats. A number of the more important prey species are found in or associated with the DSL, including barracudinas, jumbo squid, and *Gonatus* spp. squids (Anderson 1977; Magnússon 1996; Markaida and Sosa 2003; Gilly et al. 2006). That bigeye threshers feed within the DSL is consistent with the findings of the other diet studies and has been deduced based on their vertical migratory behavior. Although none of the tracking studies have been conducted within the SCB or California Current, electronic tagging data show a diel migration that seems

to parallel the migration of the DSL (Nakano et al. 2003; Musyl et al. 2004; Weng and Block 2004). In addition to foraging within the DSL, bigeye thresher sharks also appear to forage near the top of the water column. Pacific saury, Pacific mackerel, and northern anchovy are epipelagic, remaining largely in the surface-mixed layer (Jacobson 1992; Kato 1992; Konno and Wolf 1992). The final species of the top seven taxa (Pacific hake) has been characterized both as demersal and pelagic. When found over the continental shelf, it remains associated with the bottom during the day but forages in surface waters at night (Alverson and Larkins 1969; Quirollo 1992). The occurrence of this species suggests the possibility that the bigeye thresher also feeds near the benthos, similar to swordfish that feed on banks in near-shore waters (Carey and Robison 1981; Carey 1990). Finally, the presence of bocaccio, although only in one stomach, confirms the potential for epi-benthic foraging because this species seldom moves more than 10 m above the bottom (Starr et al. 2002). These behaviors are similar to those of sharks off Ecuador that also fed on epi-benthic species. The bigeye thresher is capable of foraging throughout the water column from the surface to the DSL as well as on demersal or reef-associated species.

In the SCB, the relative abundance of some of the top teleost prey species is known through larval collections taken during the annual CalCOFI cruises. Based on several egg production models, we know that larval abundance is representative of the abundance of breeding adults (Lasker 1985; Ralston et al. 2003). The standardized larval abundances of the five most important teleost prey in the bigeye thresher diet were examined in order to get an idea of whether bigeye threshers are feeding on abundant prey or specifically seeking prey that are less abundant in the SCB. While the larval counts may not reliably indicate prey that are neither spawning during the surveys nor vulnerable to the sampling gear, these counts nonetheless provide some information on the presence of the prey in the SCB. The relative ranking of larval abundances for the top teleost prey are: Barracudinas spp. – 43, 69, and 96 for three taxa identified, none of which were the duckbill barracudinas; Pacific hake – 2; Pacific saury – 81; Pacific mackerel – 21; and northern anchovy – 1 (Moser et al. 2001). Thus, the bigeye thresher diet includes the two most abundant species as well as some less abundant species. As for the cephalopod prey, recent evidence indicates that jumbo squid have been increasing in abundance throughout the California Current since 1998 (Field et al. 2007; Zeidberg and Robison 2007). It is interesting to note that the jumbo squid was not found in samples collected prior to the fall of 2005 in the present study. *Gonatus* spp. squid are the most abundant squids in the subarctic Pacific Ocean, and several species are found regularly in the California

Current waters (Anderson 1977; Okutani et al. 1988; Hunt and Seibel 2000). Without identification to the species level, however, it is not possible to know the relative abundance of those consumed by bigeye threshers in the current study.

Based on the ecology of the top prey species, it appears that many, but not all, are schooling prey. Jumbo squid, bocaccio, and king-of-the-salmon, for example, are not likely to be found in cohesive schools that are typical of anchovy and mackerel. In addition, studies in other areas demonstrated that bigeye threshers occasionally feed on benthic prey. Reportedly, thresher sharks use their long tail to stun schooling prey while foraging (Springer 1961; Compagno 2001); however, whether the tail is used to forage in all habitats is not known given that some prey may be more solitary, demersal, or reef-associated.

As previously mentioned, one aspect which limits conclusions about bigeye thresher shark foraging ecology is the lack of information on when feeding occurs. Despite suggestions that they are primarily a nocturnal species (Nakano et al. 2003), it is more likely that bigeye threshers forage both during the day and the night. During the day, their vertical range overlaps with the DSL-associated organisms found in their stomachs, and their large eyes and cranial endothermy are ideal for foraging in dark, cold waters (Block and Carey 1985; Musyl et al. 2004; Weng and Block 2004; Fritsches et al. 2005). Swordfish, which are known to forage at depth during the day, have similar adaptations (Carey et al. 1971; Carey and Robison 1981; Carey 1990; Fritsches et al. 2005). Also, the diel vertical movements are extensive and it seems unlikely that these would be undertaken solely to avoid predation, given their large size and trophic position.

Conclusions

The bigeye thresher shark appears to be more of a generalist and opportunist than the other pelagic sharks of the SCB, with the possible exception of the blue shark. A broad range of prey from mesopelagic, epipelagic, and epi-benthic habitats was observed in the stomachs of only 23 individuals. While this study provides the most detailed information on the diet of bigeye thresher sharks in the north Pacific Ocean, additional work remains. No electronic tagging studies of bigeye threshers have been conducted in the SCB. It would be of great interest to examine the vertical movement patterns for the same region where stomachs are collected. Also, conclusions about the relative importance of different prey items could be improved by estimating the weight of the ingested prey. Finally, because bigeye threshers are relatively rare in the drift gillnet fishery catch, the sample size in this study is small and covers a narrow temporal and spatial scope. If possible, a broader sampling regime would

reduce uncertainty about patterns of foraging times and depths, and allow for an examination of interannual differences and the impacts of various environmental factors and location on diet. Nevertheless, the detailed information presented is critical as we move toward multispecies assessments and a better understanding of the interactions among this top predator and its prey within the California Current ecosystem.

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